

Twenty-First Century Systematics and the Human Predicament

Paul R. Ehrlich

Bing Professor of Population Studies and President, Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305, Email: pre@stanford.edu

Systematists could play an important role in preserving biodiversity, but for the most part they have not yet done so. By creating a 21st century systematics with one major focus on that task, not only would humanity be benefited, but taxonomy itself could regain some stature among the biological sciences. Necessary steps to create such a systematics include developing methods of dealing with population diversity, concentrating effort on model groups and using them to investigate mechanisms of population differentiation, and designing a biodiversity database to answer important and interesting questions. Systematists should stop writing about the long-solved "problem" of "what is a species?" and abandon impractical plans for creating a cladistic tree of all life forms — a project that, even if it could be completed, would yield little of value. Taxonomists, like all other scientists, should be trained to sample nature in order to understand it. Systematics should be expanding its boundaries and collaborating with scientists in many other disciplines, where its knowledge and techniques can make valuable contributions to solving human problems.

The stuff we taxonomists study is disappearing at a rate unprecedented since a comet sent the non-feathered dinosaurs packing some 65 million years ago (e.g., Thomas et al. 2004). At the same time, never has the need for good systematics been more obvious and excitement in parts of the discipline more palpable. The time has come to build on that. Humanity is, after all, faced with the degradation of a crucial component of its natural capital, the populations and species that comprise biodiversity and are working parts of its life-support systems (Daily 1997). The "human predicament" is the expansion of humanity's impacts on those systems to the point where both the long-term biophysical sustainability and the socio-political stability of society are seriously threatened (Ehrlich 2000; Ehrlich and Ehrlich 1991, 2004). Perhaps the biggest challenge in achieving global sustainability that systematists and other scientists face today is finding novel ways of preserving our natural capital, especially biodiversity (e.g., Daily and Ellison 2002). By vigorously taking up that challenge, we can simultaneously create a 21st century systematics with expanded horizons, add a series of exciting problems to our research agenda, expand our collaboration with other scientists, and gain more financial and moral support for our core activities.

And why shouldn't we? After all, biodiversity is the natural domain and subject of investigation of systematics. To me, the core of systematics is the description of the past and present diversity of life (including the diversity of behaviors and interactions) and the classification of life forms, along with the development of tools for communicating about that diversity to other scientists and to the general public. Moving out from that core, systematists should naturally be concerned with, and do research on, the mechanisms that generate biodiversity and cause lineages to change through time, that create biogeographic patterns, and that cause diversity to increase or decline. That is, systematics blends at the edges with evolution, ecology, behavior, and conservation biology.

So it seems appropriate to ask why our discipline has had so little impact on public policy, even though some of the leaders in the fight to save biodiversity, for instance Peter Raven and Ed Wilson, have been systematists. Why is the general attitude toward systematics that was summarized by a journalist in the *Baltimore Sun*, in the context of a fascinating taxonomic discovery: "Today it's a backwater, ignored by students and patrons of science in favor of genetics and other cutting edge careers" (Stroh 2003)? Why, equally, has the new discipline of conservation biology been largely "captured" by ecologists, when that discipline could just as logically have been allied with systematics? Systematists are in the best position to measure what is disappearing and what is at risk; ecologists are well placed to figure out what environmental changes are causing the extinctions. By playing a more prominent role in conservation biology, systematists could have made it clear that our discipline is of great importance in dealing with the human predicament and given us more of the opportunities I mentioned above. Here I want to examine why that hasn't happened and what changes we might adopt to make it happen.

WHY SYSTEMATICS HAS NOT BEEN A FRONT LINE DISCIPLINE AND WHAT TO DO ABOUT IT

One answer is clearly that systematists, like many colleagues in other disciplines, still adhere to the antique view that scientists should abjure participating in politics or "advocacy." I've discussed this silliness elsewhere (Ehrlich 2002) and won't belabor the topic here. I'll just remind you that when an epidemiologist says that SARS is a dangerous disease and recommends quarantine, she's not accused of being an advocate. But if a taxonomist asserts that the extermination of biodiversity could threaten the human future and recommends reducing human population growth and per capita consumption among the rich, that's often labeled advocacy. Some systematists have raised important issues in the face of the extinction crisis (e.g., Vane-Wright et al. 1991), but as a group we have not involved ourselves professionally in trying to solve the predicament to the extent that ecologists have — and the efforts of ecologists have hardly been adequate.

Another problem is that museums, where many taxonomists are based, are even more conservative than universities. A main (and valuable) contribution of systematics has been through its involvement in both supporting museums (for a particularly interesting summary, see Winker 2004) and botanic gardens and increasingly turning their exhibits toward informing the general public about the importance of preserving biodiversity. But only a few systematists have directly contributed to those latter programs. In the research area, Linnaeus would feel right at home in one of today's natural history museums as soon as he acquired a dictionary of cladistic jargon, as I pointed out in a much-too-optimistic article long ago (Ehrlich 1961b). Methods of preservation of most specimens would be much the same as in 1759 — stuffed bird and mammal skins, dried insects and plants, and so on. Too little effort has been made to start supplementary collections of specimens preserved in non-traditional ways, especially of model groups. We need more samples of, for instance, entire birds and butterflies (especially hatchlings of the former and eggs, larvae, and pupae of the latter) in fixatives. And more research should be pursued on the best ways of preserving internal organs for study now and in the distant future (Ehrlich 1964). On the positive side, though, there is an important trend toward providing long-term very deep freeze storage of many organisms to provide higher quality material for molecular systematists in the future.

The sampling of nature represented by traditional collections is still usually the exact opposite of "systematic" — emphasizing "good specimens" and adults. In the past it has sometimes been openly biased. I well remember N.D. Riley, keeper of the Lepidoptera collections at the British Museum (Natural History) (now the Natural History Museum, London), bragging to me in the

1960s that for a century the Museum had been buying collections, saving the "aberrations," and discarding the "junk." There are thus no population samples at the British Museum, for example, that would permit one to determine the frequency of melanic morphs of *Biston betularia* either before or after the industrialization of Britain. There are no proper samples in U.S. museums that would allow someone to see if a coevolutionary race between *Danaus plexippus* and its mimic *Limnitis archippus* can be documented, although both have been common butterflies. Curators do not yet see as their job assembling series of samples of selected "model" organisms to create opportunities to investigate microevolution and, perhaps, help to determine the more subtle impacts *Homo sapiens* may be having on the rest of biodiversity.

But I think the most important reason that systematics has had little impact on the preservation of biodiversity (and is ignored by most other biologists) is the narrow intellectual focus of the discipline. I believe there are many things we systematists could do to make our discipline more relevant and to increase its credibility with scientists and the public. One is to focus much more on the non-core aspects of our disciplinary mission — to employ that essential core as a launch pad for dealing with important theoretical questions in biology and crucial aspects of the human predicament. In the process of doing that and reallocating the efforts of systematists, I believe we will contribute much more to dealing with the sixth extinction. And it is my firm belief that systematists (and evolutionists and ecologists, as well as many other scientists) have an ethical obligation to put some substantial part of their professional effort into dealing with that extinction and other aspects of the human predicament.

The time is ripe for broadening and refocusing; where systematics is going is a pressing and relatively widely recognized question (e.g., Mallet and Willmott 2003). I suggest the following major changes:

1. Focus our theoretical thinking on the critical conservation issue of dealing with population diversity and on explicating the complexities of population differentiation.
2. Ask ourselves what kind of biodiversity database will scientists need fifty years from now, and what could and should systematists contribute to it? Then mount a major effort to create it.
3. Expand the frontiers of our discipline to encourage more collaboration with other scientists, from molecular biologists to linguists.
4. Overall, create a "21st century systematics" to replace the once forward looking "new systematics", now well over six decades old (Huxley 1940). Insure that a major occupation of 21st century systematists is to help preserve biodiversity through targeted research and public education.

Other biologists can help encourage these changes both by learning more about the important ways in which systematics can expand our understanding of the world and giving moral support to those systematists who do "think big."

I'll now expand on these points.

FOCUS MORE ON POPULATIONS

One thing new systematists would do is cease the interminable armchair discussions of the definition and "nature" of species, and perpetually renaming them. The brilliant system developed by the Swedish botanist Carl Linnaeus (e.g., 1758) provides the foundation for biological nomenclature (Mayr et al. 1953). It has served science well for almost 250 years, but has not proven uniformly satisfactory (no taxonomic system could be) because of the many roles it must play. The system must communicate about multidimensional sets of morphological, behavioral, and genetic relationships, a process that always involves making arbitrary divisions in continua of evolutionary differentiation. The issue of the definition of species never concerned Linnaeus (who simply

took them for granted), but was given impetus by Darwin's choice of title for his classic work (Darwin 1859), and interested world-class biologists in the past (Dobzhansky 1937; Mayr 1942, 1957, 1963). It attracted much attention from philosophers (e.g., Ghiselin 1975; Hull 1976; Ruse 1987), mostly after it was no longer an appropriate focus for biological investigation, since the issue of "what is a species" was definitively recognized as insoluble (or, rather, badly posed) forty years ago. This is a point worth expanding, because one barrier to creating a 21st century systematics are the opportunity costs of smart-but-insular systematists beating this long dead horse.

The Species Problem

Research by my group on checkerspot butterflies played a role in demonstrating that the species "problem" was a non-problem, at least from the viewpoint of evolutionists and ecologists. First, a phenetic analysis of *Euphydryas editha* and *E. chalcedona* specimens (Ehrlich 1961a) showed that individuals assigned to two different species were related to each other in a variety of ways, showing different degrees of similarity. At that time it was also made clear that the genus *Euphydryas*, as well as a very large proportion of other Nearctic butterflies, did not divide neatly into distinct species (Ehrlich 1961a), a result that continuing investigations of *Euphydryas* assigned to the species *E. chalcedona*, *E. anicia*, and *E. colon* has abundantly confirmed (e.g., Brussard et al. 1989). Then, the discovery of the diversity of habitats, flight periods, oviposition plants, secondary host plants, nectar sources, population sizes, and population control factors among *E. editha* populations demonstrated that species comprised of genetically rather similar populations (Baughman, et al. 1990), were not necessarily ecological units (Ehrlich and Hanski 2004; Ehrlich, et al. 1975). And, finally, research on *E. editha* also showed that the genetic coherence of that species could not be credited to gene flow uniting population gene pools (Ehrlich and Raven 1969; Ehrlich and White 1980). The generality of this conclusion has not yet been established (Rieseberg 2001), so that the degree to which populations within a "species" in sexually reproducing organisms "evolve collectively" (Rieseberg and Burke 2001) should remain an important topic of research.

The basic reason that checkerspots (and the rest of the natural world) are not divided into easily-identifiable unambiguous units is, of course, that the dominant process of speciation creates continua of geographic differentiation. Such continua are displayed throughout Earth's biota in general (Ehrlich 1961a), and the checkerspots provide excellent examples. Phil DeVries, in his outstanding treatise on Costa Rican butterflies (1987:202), comments extensively on the difficulties of determining what should and should not be considered species in one group of checkerspots, the Phycioiditi (*Eresia*, *Anthanassa*, *Phyciodes*, etc.), and the problem with the Phycioiditi carries over into the Nearctic realm (e.g., Scott 1986:309-312).

Early phenetic results demonstrated the existence of continua of geographic differentiation; more recent research has shown that the same applies broadly to genetic differentiation as well. For instance, almost continuous degrees of genetic divergence are exhibited by checkerspot populations, regardless of which particular genes and populations are examined or method of analysis is employed (Baughman, et al. 1990; Brussard, et al. 1989; Brussard, et al. 1985; Wahlberg and Zimmermann 2000). Most evolutionists studying sexually reproducing organisms (especially animals) are satisfied to follow Ernst Mayr's (1942) lead and define as distinct species populations that are sympatric without showing abundant signs of hybridization, be they populations of lions and leopards, gold-crowned and white-crowned sparrows, or of *Euphydryas aurinia* and *E. maturna*. This sensibly recognizes the evolutionary importance of separate gene pools, even though technically determining the amount of interbreeding and hybridization can be complex (Ehrlich 1961a; Sokal and Crovello 1970). But when it comes to allopatric populations, the task of employing the

"potential interbreeding" criterion of the so-called "biological species concept" becomes impossible in all interesting cases (Ehrlich 1961a; Ehrlich and Holm 1962). Tests conducted in experimental sympatry can, of course, in some cases allow reasonable predictions of what actual interbreeding might occur in populations remigrated into sympatry in some at-the-moment undetermined selective environment in nature. Recently illuminated examples, such as the possibility that differentiated chimp and "human" lineages might have interbred for 3 million years after initial divergence (Navarro and Barton 2003; Rieseberg and Livingstone 2003) underline the problem of when and where to draw species boundaries under such criteria.

Plant biologists have not been over-concerned with species definitions in general, and the biological species concept in particular (e.g., Raven 1978, 1980a). Indeed, when asexual and fossil organisms are considered, it has long been obvious that what biologists call "species" are not all biologically equivalent entities. No narrow species definition will ever serve all purposes, and this is becoming widely recognized (e.g., Hull 1997). The definition used in any particular case depends on the question to be answered, and in some cases increasingly satisfactory solutions can be found (e.g., Sperling 2003). The best broad definition of species is simply "kind," for which might eventually be substituted some arbitrary level of phenetic or genetic divergence. Kind, in fact, has proven a quite useful definition in practice for both sexual and asexual organisms, because evolutionists, ecologists and behaviorists usually know what sort of entity is being discussed, and someone "twitching" birds or butterflies on a life list ordinarily doesn't care. The same can be said for cryptic kinds that can only be separated by biochemical techniques, a phenomenon that is likely to be very widespread (for a recent example, see John Burns' and Dan Janzen's work described in Pennisi 2003).

Despite all this, as late as 1998 one taxonomist was able to write "What is a species?" is considered one of the central issues of biology as well as one of its most vexing problems" (de Queiroz 1998:72). Another taxonomist expressed the view that the "nature of speciation processes can only be investigated and understood when there is agreement on the nature of species" (Claridge 1995:38). In fact, the vast majority of biologists pay not the slightest attention to the "problem" of "What is a species?" One might better stand Claridge's argument on its head and say that we'll understand much more about the variety of entities we conveniently call species when we more thoroughly understand the processes of population differentiation. Substantial progress has been made in elucidating that differentiation by scientists who are not deterred because species are named for convenience in communication and are not all presumed to be the same kinds of entities (e.g., Bush 1994; Coyne 1992; Ehrlich and Raven 1969; Grant and Grant 1997; Kaufman, et al. 1997; Orr 2001; Orr and Smith 1998; Rieseberg 2001; Schwarzbach and Rieseberg 2002; Turelli, et al. 2001; Via 2001; Wu 2001). What would we think if Earth scientists were perpetually wondering "What is a mountain?" and writing papers talking about "good mountains" and "bad mountains" and analyzing different "mountain concepts" instead of focusing, as they have, on different forces in orogeny and erosion? What if they stated that the nature of processes responsible for topographic relief can only be investigated and understood when there is agreement on the "nature of mountains"? For a tiny sample of the more recent literature on the species non-problem, see Mischler and Donoghue (1982); Cracraft (1983); Patterson (1985); de Queiroz and Donoghue (1988); Nixon and Wheeler (1990); Vrana and Wheeler (1992); Vogler and DeSalle (1994) Mallet (1995); Davis (1996); Avise and Wollenberg (1997); Claridge et al. (1997); Mayden 1997; Harrison (1998); Sterelny and Griffiths (1999); and Hey (2001).

Nothing I have said here should be interpreted as demeaning the fundamental importance of investigating the processes of population differentiation. Among other things, understanding them will help us better evaluate the sorts of processes that need to be protected in order to permit the

continued generation of diversity — something that could be vital to restoration biology. In any case, it is clear that we still suffer from a lack of information on population differentiation in nature, where the few detailed studies that have been done (e.g., Ehrlich and Hanski 2004) suggest that species are much less unitary entities than museum and laboratory research suggests. It may be a hopeless suggestion, but I would prefer that the phrase “population differentiation” increasingly substitute for “speciation.” It would get away from the psychological need, which seems to persist, to define species as all the same sorts of units, such as “the most inclusive entities that directly participate in evolutionary processes” (Rieseberg and Burke 2001).

The dominant species-centric biodiversity paradigm (e.g., Claridge et al. 1997) has unfortunately resulted in an emphasis in conservation biology on the preservation of species, and thus helped perpetuate the neglect of the equally important (in many cases more important) issue of the preservation of populations (Ehrlich and Daily 1993; Hughes et al. 1997; Hughes et al. 1998) and, thus, ecosystem services (Daily 1997). That has been a distinctly negative (if inadvertent) impact of systematics on the conservation of biodiversity.

Subspecies and the Systematics of Populations

A question long debated by taxonomists and of interest to conservation biologists is whether or not to recognize taxonomic entities below the level of species. That subspecies are not ordinarily evolutionary units (because of discordant character variation) was pointed out 50 years ago by Wilson and Brown (1953), and studies of butterflies (e.g., Gillham 1965), including some by our group on checkerspots (e.g., Baughman et al. 1990; Brussard et al. 1989), have supported this view. There is, of course, considerable interest in studying patterns of genetic variation within species (Avice 1994), and in some circumstances subspecies names can make biogeographic and phylogeographic discussions smoother. But there is usually only one reason to name and describe new subspecies today — and it is connected with the human predicament. In some circumstances, populations in danger of extinction can be protected legally if they are designated as subspecies. That utility would disappear if more sensible laws aimed at preserving humanity’s natural capital were put on the books. Unhappily, rather than just making that designation when it appears worth the effort, taxonomists have been pushed into a biologically empty debate about what is an “evolutionarily significant unit” within a species (Moritz 1994; Ryder 1986) by the needs of policy makers to come up with rules for what entities to protect. As Tom Brooks cogently put it, at the global scale this amounts to “fiddling while Rome burns” (quoted in DeWeerd 2002) — but some fiddling may actually help quench a few local blazes.

It is a major challenge for 21st century systematics to find scientifically sound new ways of dealing with the systematics of suites of populations, in the process providing a more rigorous basis for monitoring (and countering) the ongoing decay of population diversity. For too long the magnitude of biodiversity loss has been measured by the rate of species extinctions, an approach that understates the seriousness of the problem and masks some of its most important consequences. A 21st century systematics of populations would take into consideration changes in their numbers, dynamics, distributions, and genetic compositions, as well as the consequences of such changes for ecosystem functioning and the delivery of ecosystem services (e.g., Luck et al., in press). And at the population level, as at the species level, a modern systematics would necessarily sample nature, not attempt to be comprehensive. Even large-scale application of ever-more-automated molecular fingerprinting techniques will not allow monitoring of more than a tiny fraction of the billions of natural populations. When one considers how much is already known about population and metapopulation structures in checkerspot butterflies (Ehrlich and Hanski 2004), and how much

more there is to discover, it becomes crystal clear that population systematics can be developed for only a tiny and carefully selected subset of populations.

BUILDING THE BIODIVERSITY DATABASE

It is high time that systematists organize themselves to create a database that will be useful throughout biology. It will be a very large task, but it will focus the efforts of the discipline and place it in its rightful position within biology — the most important sciences of the 21st century. But in the process systematists should keep in mind three very important tasks.

Do more to stabilize nomenclature. We can't build a successful biodiversity database without greatly reducing the near constant changing of names of taxa that infests systematics. The names we use must be understandable not only to systematists, but to the other scientists who will be major users of the database and to the general public. My recent experience with a many-authored book on checkerspot butterflies (Ehrlich and Hanski 2004) demonstrates the basic utility of the Linnaean nomenclature system for communication among scientists. Fifteen co-authors had no difficulty letting each other know exactly which organisms were being discussed, and were perfectly relaxed about the ambiguities that are inevitable when imposing a discontinuous system of names on a natural system that is permeated with various continua. And our colleagues who work on other systems should easily understand to which organisms, checkerspot, host plant, or whatever, we are referring. The same can be said for the communication among specialists about butterflies in general in symposia and in the production of a recent book on the entire butterfly model system, spearheaded by Carol Boggs (Boggs et al. 2003).

Indeed, if those interested in biology had stuck to the Linnaean system (originally designed for international communication), treated the expanded Linnaean hierarchy conservatively (Ehrlich and Murphy 1981), and changed names only *in extremis*, our job would have been even easier. The multiplicity of "scientific" and artificially generated "common" names (Murphy and Ehrlich 1983), and the instability of both, is a central reason that systematics is an unappreciated discipline. Most scientists and nature lovers are only exposed to it in the form of very frequent, very annoying, and often senseless, changing of names. Worse yet, the discipline is now debating changing all names, including all species names, to ones based on the uncertain and (for communication) relatively uninformative estimates of recency of common ancestry (Donoghue 2001; Pennisi 2001). Most people, including most biologists, are not much interested in relationships based on relative times of divergence. They care little when the lines leading to birds, crocodiles, and lizards split from one another — they are much more concerned with communicating about the phenetic relationships of those organisms, the phylogenetic relationships that are based on time and rate of evolution. Told that a "Birdcroc" is sneaking up on her, a naturalist wouldn't know whether it would sing her a song or drag her into the lake and eat her. This means (horror of horrors) that for communication with non-systematists, I'm in favor of retaining paraphyletic taxa.

This is a topic on which reasonable people can differ, of course. One can argue that, if a well substantiated branching tree of life can be created, that a more stable nomenclature could be based on it, with the standard of monophyly adopted throughout. This would ignore the rate aspect of evolution, but its basis would be clear. But would such a system be practical to create? It is one thing to estimate branch-time trees for a sample of biodiversity, and then compare them to phenetic trees to get some idea, for instance, of how frequently there are very rapid radiations. It would be quite another to try to work out branch times for all taxa, even just going up to the genus level. I don't think it would be worth the effort. But it would be worth the effort to develop and use some sort of coding system for at least base taxa (individuals, populations, species) for the biodiversity

database. These could supplement the use of the Linnaean system and be used by the database's gatekeepers to route incoming data properly.

In any case, as long as the Linnean system is the main one in use, every effort should be made to avoid changes in the latinized names of obligatory categories, and journals should refuse to publish any name changes that do not reflect stunning new results (i.e., at the level of finding out that two "species" are actually males and females of the same population). Changing the status of allopatric populations wouldn't ordinarily qualify, nor would deciding a genus was only a subgenus or vice-versa. Only a handful of people care at all whether *Euphydryas anicia* is a "good species" or a "subspecies" of *Euphydryas chalcedona*, and the question is close to meaningless in any case.

So what to do? Some steps could be relatively simple. Coining of more common names should cease; *Euphydryas* or *Castilleja* is no more difficult for a layperson to learn than hippopotamus or chrysanthemum. Once a system of database codes are agreed upon, stabilization committees should be established for all major (especially model) groups, whose first charge will be to approve the names of all lower taxa within that group and match them to the biodiversity database codes. That would both help to avoid name-changing that would confuse non-systematist contributors to, and users of, the database, and would minimize the inevitable mis-assignment of data. Remember that the vast majority of specific names are never used in a context where using a different name would make the slightest practical difference. Indeed, it would be interesting to see if the majority of specific names are ever used beyond the original description and subsequent catalogues and taxonomic re-shufflings. Above all, systematics should reduce its focus on names (or bar codes, or whatever) that we use as "convenient landmarks in the continuum of life" (Ehrlich 1961b) and concentrate more on keeping that continuum going and elucidating the kinds and mechanisms of its differentiation.

Recognize that "completely" describing the tree of life is impossible. Some believe that the task of systematists "is to chart the diversity of life, in its entirety, from the tiniest tips of the tree to every one of its branches" (Donoghue 2001:755). Of course, technically the tiniest tips (twigs) of the tree are all individual organisms, recent and past, that are post-reproductive or died without leaving offspring (I am a twig!). But knowing the context, we can assume that the statement refers to species (however defined) as "tips," and "to chart" includes writing superficial species descriptions and arriving at some sort of estimate of times of occurrence of the myriad fuzzy crotches of the phylogenetic tree. Even completing the job using species as the tips would still be quite an ambitious, and in my view scientifically questionable, project. Species are often not unitary "tips" — ecological or genetic units — but rather complexes of interrelated entities in constant flux as environments change. Demographic units go extinct and are reestablished, and populations evolve in response to varying selection and migration pressures and genetic drift (Ehrlich and Hanski 2004). To paraphrase Heraclitus, "you can't collect the same species twice."

Systematists should be more evolutionary. Describing the nature of the twigs of the tree today at the population level (e.g., population and metapopulation demographic and genetic structure), has barely begun, even for model systems. And definition (and temporal estimation) of the crotch is fraught with problems. Long ago, simple analysis showed how futile a goal was the "complete" charting of continuously evolving life — even before its complexity was understood as it is today (Ehrlich 1961b, 1964). In the light of the accelerating extinction crisis, that goal now looks particularly ludicrous, and the opportunity costs of trying to achieve it substantial. Furthermore, that description, if miraculously achieved, would be instantly obsolete and unlikely to do much help solve the human predicament.

Start sampling nature in order to understand its diversity better. Because of the lack of well-designed, taxonomically and geographically stratified sampling, many major systematic questions

are not much closer to solution today than they were in 1950. Fortunately, there is movement in the direction of judicious geographic sampling, as exemplified at the California Academy of Sciences, with its emphases on expeditions to key places such as Madagascar, the islands of the Gulf of Guinea, and Yunnan in China.

It is now much too late to expand our knowledge of biodiversity much by continued random additions to the existing crude systematic/genetic/ecological/behavioral overview of the vast panoply of biological diversity. A major, well-funded effort could help (Raven and Wilson 1992), but that effort does not seem to be feasible politically because it has no obvious scientifically or practically useful goal. Still, as I have emphasized elsewhere (Ehrlich 1997:23–33; Ehrlich 2001), it is not too late to develop a substantially more detailed and useful understanding of a limited number of model groups — comprehensive pictures of their diversity, distribution, and ecological relationships (see also Raven 1980b). We know little about the degree to which species in most groups are or are not ecological units or genetic units (bound together by gene flow). The investigation of population and metapopulation diversity has barely begun. Systematists have only a rough idea of the relative diversities of major taxa in various communities. The issue of dissonant phenetic evolution of life-history stages has barely been explored.

Deep knowledge of sample groups could begin to answer questions in those areas. It could also help in plotting strategies for conserving biodiversity and honing human judgments on key questions such as taxonomic substitutability (redundancy) in ecosystem services, central issues in solving the human predicament. It could make estimation of extinction rates more precise. It could also help highlight a less-appreciated aspect of the human predicament — the enormous loss of Earth's heritage of information as expansion of human activities deletes much of the “experience” stored in DNA as a result of eons of evolution (loss of the diversity of human languages is an analogous tragedy now well under way). Thorough understanding of some model groups could provide a framework of understanding for population biologists in a century or so when much of today's biodiversity will exist only as museum specimens or fossils. Think of how much better we would understand processes of the diversification of life and our own origins if we had comprehensive studies, done at the time, of Cretaceous dinosaurs, birds, and plants — or of the primates of eight million years ago (when the common ancestors of chimps and people were alive)!

A database to assemble comprehensive information on a well-stratified sample of taxa could make a big contribution toward generating answers to many important questions in biology in general and conservation biology in particular (Ehrlich 1997; Sisk et al. 1994). One step in that direction is represented by the NSF's “Tree of Life” program (www.nsf.gov/pubs/2004/nsf04526/nsf04526.htm; <http://tolweb.org/tree/phylogeny.html>), which focuses on the “phylogenetic resolution of large lineages or clades,” but imagines it will eventually deal usefully with 1.7 million species. Describing the relatively permanent basic architecture of a tree is feasible and reasonable (for a recent fine example, see Feild 2003); describing it down to its tiniest, ever-changing twigs is neither. With the *Tree of Life*, and related efforts like that of Brent Mishler and his colleagues (Mishler et al. 2003), to create phylogenetically structured databases, a framework for organizing our samples of biodiversity may already be emerging. Building on that framework to produce a useful tree of life would be an ideal megaproject for 21st century systematics. It would need to be much more focused than an attempt at creating a complete list of species and an indication of their putative cladistic relationships. The megaproject could broaden systematics by establishing many contact points with the geneticists, ecologists, developmental biologists, neurobiologists, behaviorists, climatologists, GIS specialists, soil scientists, hydrologists, oceanographers, and other researchers. The other scientists could both contribute data and work with the database. Computer scientists, in turn, could aid in making the database the state-of-the-art standard.

The database should be designed for problem solving, and its creation would be a cooperative venture whose appeal would in part be its demonstration of the tight interdisciplinary connections that more and more are features of modern science. It would put systematics at the center of things rather than the periphery. Two questions posed to me recently could be almost instantly solved if such a database existed with butterflies, ants, birds, and mammals included as well-developed sample groups, and appropriate geographic and morphological data were included. They were: (1) how frequently is topographic heterogeneity a key to persistence of populations of small-bodied animals? and (2) is the forward position of the clitoris in bonobos and people an adaptation to facilitate female-female bonding? All of you can think of many other interesting questions, and other sorts of data that, if included in the database, would be helpful in answering them.

The criteria for selection of model systems to build into the database should be under continuous discussion, but would include sampling of ecological, geographic, and systematic diversity, direct importance or interest to human beings (including through the delivery of ecosystem services), and potential for "completion." Groups that might be chosen under the potential-for-completion criterion today include most vertebrates, vascular plants, and, my own favorite group, butterflies. The Papilionoidea are the most obvious taxon of the invertebrates to select as a model group for accelerated systematic, ecological (including ecophysiological), evolutionary, and behavioral study. Butterfly researchers already recognize this (Boggs, et al. 2003; Ehrlich and Hanski 2004; Watt et al. 2003), and it is to be hoped that many more systematists can be recruited to their ranks. Butterflies also can serve as a wedge to break the tendency of conservation groups and governments to concentrate their attention on vertebrates — an egregious error in a world where preservation of ecosystem services must be a conservation priority.

Birds, butterflies, and mammals deserve more attention because amateurs can easily be co-opted into efforts to comprehensively understand them, and because of their symbolic and ecotouristic importance (but see, Sekercioglu 2002). Other relatively well-understood arthropod groups that might serve as models include ants (Beattie 1985; Gordon 1999; Hölldobler and Wilson 1990), because of their incredible importance in ecosystem functioning, especially in the tropics; bees because of their key roles in pollination (Michener 1974, 2000); mosquitoes, ticks, and other organisms of public health importance, and tiger beetles, which have many attributes that would make them good indicators of biodiversity (Pearson and Cassola 1992) and would serve, as predacious insects, to provide a nice comparison to the butterflies. In terms of the human predicament, attention to organisms that are vectors or reservoirs of pathogens, and to the pathogens themselves is especially important in view of the deteriorating epidemiological environment (Daily and Ehrlich 1996a).

Focusing attention on understanding already well-studied groups has several enormous advantages. First, in some sense it is possible that we'll be able to "complete" them — providing comprehensive pictures of the evolution of at least a sample of branches on the tree of life. Efforts to "complete" the taxonomy of vascular plants are well under way, centered in institutions like the Missouri Botanical Garden, the Royal Botanic Gardens, Kew, and the New York Botanical Garden, and important issues in the origin and evolution of the flowering plants are gradually being elucidated (Ackerly et al. 2000; Friedman and Floyd 2001). Every time a new detailed study of the systematics of a butterfly group appears (e.g., Penz 1999; Penz and DeVries 2003), we inch further out on the asymptote of understanding a classic model taxon (Boggs et al. 2003). Even among vertebrates, great opportunities obviously remain for expanding knowledge of their diversity and patterns of radiation (e.g., Mayr and Diamond 2001; Meegaskumbura, et al. 2002), and some of the work on phylogenetics of large vertebrates may eventually prove useful in interpreting the human past (e.g., Hassanin and Douzery 2003).

All of this does not mean that I think all revisionary and exploratory work should be done on model systems. Whenever I look at a sample of gorgeous and diverse tropical Hemiptera or Hymenoptera, or even subalpine flies (Hughes, et al. 2000), my taxonomizing instincts rise to the surface and my mind is flooded with phylogenetic questions. Surely all of us should spend some time exploring, asking questions, doing research, and enjoying organisms that are not necessarily suited for use as model systems (but may have overlooked potential in that area). And data from such exploring could be integrated into the database. But in my view that does not free us of an obligation to our discipline and to humanity to put some substantial portion of our effort into more deeply understanding those important samples of biodiversity.

EXPAND THE BOUNDARIES OF OUR DISCIPLINE

There are steps beyond creation of a comprehensive biodiversity database that would help to expand the usefulness, recognition, and support of systematics. One would be to expand collaborations with molecular biologists and make sensible use of genomic information. Techniques developed for systematics have certainly been essential to biologists with an interest in molecular evolution (e.g., Felsenstein 1985; Harvey et al. 1996), and molecular data have been central to efforts of systematists to sort out the patterns of phylogenetic branching, most famously in the recent branches of our own family tree (e.g., King and Wilson 1975; Krings et al. 1997). But two related erroneous ideas now combine increasingly to constrain and marginalize systematics. One, of course, is that temporal relationships based on splitting time are the only important aspects of phylogeny (see discussion in Ehrlich 1997:23ff). The other is that information on nucleotide sequences is somehow more important or fundamental than information on any other aspect of the phenome (Ehrlich 1964) (the genotype is the information coded into the nucleotide sequence, but the sequence itself is part of the phenotype). The additional systematic information provided by DNA should not be used as the primary basis of general taxonomic classifications (Tautz et al. 2003), as Christopher Dunn points out (2003). But its value to taxonomy and in systematics related to conservation (e.g., Baker et al. 2003; Baker et al. 2000; Baker and Palumbi 1994, 1996; Palumbi and Cipriano 1998) can hardly be overestimated.

How sequence information should be employed depends on the kinds of questions being asked. Phenetic relationships are often more useful to understand than branching times (as in the bird-crocodile case) — phylogeny does, I repeat, have both rate and time dimensions (see also Lipscomb et al. 2003; Seberg et al. 2003). In the case of nucleotide sequences, information on aspects of the phenome other than those sequences may be much more instructive. For instance, the small sequence differences between chimps and people so far have been of little interest to scientists (except for surprise at the paucity of differences and a growing fascination with the developmental issues thus raised) as compared to the morphological and (especially) behavioral differences and similarities of the two organisms. On the other hand, recent work showing that the skipper butterfly, *Astraptes fulgorator*, is actually a complex of perhaps ten or more sibling species (Pennisi 2003; Stroh 2003) casts new light on a significant puzzle in plant-herbivore coevolution. If systematics is to thrive, it must place the important topics of branching times and sequencing into the perspective of a broader 21st century systematics and focus on them primarily when they can be used to answer important questions.

Furthermore, molecular systematics is opening the equivalent of a vast new area to taxonomic, evolutionary, and ecological exploration. Collaboration with microbial ecologists and evolutionists in examining the taxonomic structure of the worlds of Archaea and Bacteria (rather than the two specialized offshoots of the Eucarya where most of us have concentrated our efforts) seems

sure to yield fundamental insights into the structure and evolution of the main body of biodiversity (e.g., Pace 1997). It's as if there were a whole new planet of organisms barely explored, in a pre-Linnaean state, about which one might develop novel taxonomic ideas. If systematists don't get more involved in this exciting enterprise, then they will be left behind here too as others proceed to ask the critical questions (Bohannon and Hughes 2003; Horner-Devine et al. 2004; Horner-Devine et al. 2003).

Systematists should also start more research on problems of broad interest to other biologists and other scientists. A 21st century systematics would have the potential of capturing much more relevance and interest if it expands its disciplinary boundaries far beyond routine description and the hypothesizing of branching-time relationships that preoccupy so much of the discipline today. Systematics has had too much of a tendency to be a stand-alone science. Just as world-class ecology is now interfacing with atmospheric chemistry, climatology, economics, and environmental engineering (to name a few), a 21st century systematics would feature many more collaborations with ecologists, evolutionary geneticists, conservation biologists, developmental biologists, neurophysiologists, linguists, cultural anthropologists, philosophers (especially in this age of deconstruction), and so on.

Much more of the focus of 21st century systematics, as indicated in the database discussion, could be on contributing systematic (both phenetic and branching-time) insights into the evolutionary structure of carefully selected model groups, and collaborating more closely with the molecular geneticists now attempting to look in detail at patterns of population differentiation. As other examples, the new systematists could do comprehensive censuses of a stratified sample of "May plots" in order to get an comprehensive view of the ratios of species diversities of various taxa (e.g., May 1988), and to examine carefully the systematic assumptions built into such ratios (i.e., how species and higher taxa in the surveys are to be defined). Twenty-first century systematists could promote and control the global terrestrial monitoring system I proposed earlier (Ehrlich 1997:80–83); that would be "big science" with a critical importance.

Systematists could reexamine many issues related to measures of community diversity by including the phenetic dimension of diversity (e.g., Hendrickson and Ehrlich 1971). After all, in the metrics normally used by ecologists, a lizard community consisting of six *Anolis* species is fully as diverse as one containing one *Eumeces* species, one *Cnemidophorus*, one *Phrynosoma*, one *Sceloporus*, one *Heloderma*, and one *Anolis*. Systematists could also put more effort into examining the degree to which morphospecies can reasonably be used to assess conservation situations where conventional taxonomic treatments are not accessible; indeed, much of the pioneering systematic work on monitoring has been done by non-systematists (Beattie and Oliver 1994; Daily and Ehrlich 1996b; Oliver and Beattie 1993, 1996a, 1996b). And they could extend the standard taxonomic process of mapping species distributions (think of all those maps with black dots) to use new techniques to predict distributions as functions of the abiotic environment (e.g., Fleishman et al. 2003) or more complete habitat information. The latter is being pursued at a very high level at CONABIO, the Mexican biodiversity institute. Among other things, the Mexican scientists are using the new techniques to predict rates of invasion of *Cactoblastis cactorum*, which threatens to be a serious agricultural pest in Mexico, and of Chagas disease, a potentially nasty public health problem. The techniques are also being used to judge where release of certain genetically-modified crop strains are permissible, and to determine locations of possible suitable habitat patches for the endangered swallowtail butterfly, *Baronia brevicornis*, (Jorge Soberon and José Sarukhan pers. commun.).

The 21st century systematists could have as a major goal developing new model systems to explore novel and interesting ecological questions. An important current example is the work of

John Thompson and his collaborators on selection mosaics and coevolutionary hotspots (e.g., Thompson 1994; Thompson and Cunningham 2002). Their work, and that of others (e.g., Benkman et al. 2001; Hochberg and van Baalen 1998; Zangerl and Berenbaum 2003) has been demonstrating that in addition to species not being ecological units, their coevolutionary interactions also often vary from population to population. For instance, Benkman and his colleagues (2001) have shown, largely by analyses of geographic variation in crossbill bills and conifer cones, that the coevolutionary interactions of crossbills and conifers vary from population to population, at least partially in response to the presence or absence of the red squirrel (*Tamasciurus hudsonicus*), a crossbill competitor. The consequences for the human epidemiological environment of potential population-level differences in pathogen-*Homo* or pathogen-reservoir coevolution have barely begun to be explored and would be a highly relevant field for investigation by 21st century systematists. So would targeted studies of such crucial complexes as hantaviruses and their muroid hosts (Yates et al. 2002).

One substantial opportunity for new systematists to find funding for relevant research would be through the National Ecological Observatory Network (NEON) being promoted by the National Science Foundation (<www.nsf.gov/bio/bio_bdg04/neon04.htm>). At the moment the projected role in it for the systematics community shows no grasp of how one should actually approach an important scientific problem — in this case how best to monitor changes in biodiversity, determine their causes, and project the magnitude and directions of future changes. (<ibrcs.aibs.org/reports/pdf/NEON5_June2002.pdf>). Twenty-first century systematics should be at the forefront of developing the most cost effective (as opposed to instrument-intensive) ways of accomplishing this.

Finally new systematists should expand the search for other disciplines in which systematic techniques can be applied. One obvious area to be mined is in cultural microevolution (Ehrlich 2000:228–229). We need to know much more about how languages, religions, norms (e.g., attitudes toward aggression and civil rights), and so on evolve. It is an area where the approaches and ideas of systematists could have great impact — if we remove our disciplinary blinders and give it a try. One important way to get rid of those blinders, and one where other biologists can help, is to start holding more joint meetings of systematists with ecologists, evolutionists, conservation biologists, social scientists, and others. That would promote interdisciplinary thinking, enrich two or more disciplines at once, and (if properly structured) lead to a broadening of graduate training in systematics — which may be the most critical of all needs in reforming the discipline. One can imagine the shrinkage that would occur in the “what is a species” literature if every systematist, as part of his or her graduate work, were required to do an appropriate field project on population differentiation in a model group.

CREATING A 21ST CENTURY SYSTEMATICS SHOULD BE FUN

In closing, let me note that continuing to name and estimate phylogenetic branching times for random parts of organic diversity is at least as reasonable a thing to do as was (is) describing and naming geographic features of Earth or stars in the heavens, or cataloguing a rich and unique library. It would be great to have the capability of somehow storing and making accessible life's entire DNA library and the information stored as myriad phenotypes. Naming and cataloguing is also fun, and we all should have some fun in doing our science. If working out branching times for a group of Amazonian mites or New Guinea midges is your thing, then by all means — enjoy! But put at least some of your time into research that will be more likely to aid directly in solving the human predicament. As I hope I've indicated, there are plenty of such activities for 21st century

systematists, where important questions can be asked, important hypotheses tested, and, above all, results pertinent to the preservation of biodiversity obtained. That preservation is the most critical and difficult goal of 21st century systematics — if we don't succeed, there soon will be no basis for answering any crucial scientific questions systematists have not yet recognized. Saving biodiversity and dreaming up and answering those questions are our job; they will allow future generations of systematists (and other people) to enjoy Earth's living heritage and have more fun. So let's get on with it.

ACKNOWLEDGMENTS

Some of the material in this paper is based on discussion of similar issues in Ehrlich, et al. (2004). I want to thank David Ackerly, Carol Boggs, Gretchen Daily, Anne Ehrlich, Nina Jablonski, Charles Michener, Peter Raven, and Ward Watt for reading and criticizing this manuscript. Ward has worked very hard to sharpen my arguments, even when he doesn't necessarily agree with my positions, and I'm especially grateful to him. Needless to say, the responsibility for any errors or incorrect views is mine, and mine alone.

LITERATURE CITED

- ACKERLY, D.D., S.A. DUDLEY, S.E. SULTAN, J. SCHMITT, J.S. COLEMAN, C.R. LINDER, D.R. SANDQUIST, M.A. GEBER, A.S. EVANS, T.E. DAWSON, AND M.J. LECHOWICZ. 2000. The evolution of plant ecophysiological traits: Recent advances and future directions. *BioScience* 50:979–995.
- AVISE, J. 1994. *Molecular Markers, Natural History, and Evolution*. Chapman and Hall, New York, New York.
- AVISE, J.C., AND K. WOLLENBERG. 1997. Phylogenetics and the origin of species. *Proceedings of the National Academy of Sciences USA* 94:7748–7755.
- BAKER, C.S., M.L. DALEBOUT, S. LAVERY, AND H.A. ROSS. 2003. www.DNA-surveillance: Applied molecular taxonomy for species conservation and discovery. *TREE* 18:271–272.
- BAKER, C.S., G.M. LENTO, F. CIPRIANO, AND S.R. PALUMBI. 2000. Predicted decline of protected whales based on molecular genetic monitoring of Japanese and Korean markets. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 267:1191–1199.
- BAKER, C.S., AND S.R. PALUMBI. 1994. Which whales are hunted? A molecular genetic approach to monitoring whaling. *Science* 265:1538–1539.
- BAKER, C.S., AND S.R. PALUMBI. 1996. Population structure, molecular systematics, and forensic identification of whales and dolphins. Pages 10–49 in J.C. Avise and J.L. Hamrick, eds., *Conservation Genetics: Case Histories from Nature*. Chapman and Hall, New York, New York, USA.
- BAUGHMAN, J.F., P.F. BRUSSARD, P.R. EHRlich, AND D.D. MURPHY. 1990. History, selection, drift, and gene flow: Complex differentiation in checkerspot butterflies. *Canadian Journal of Zoology* 68:1967–1975.
- BEATTIE, A.J. 1985. *The Evolutionary Ecology of Ant-Plant Mutualisms*. Cambridge University Press, Cambridge, England, UK.
- BEATTIE, A.J., AND I. OLIVER. 1994. Taxonomic minimalism. *TREE* 9:488–490.
- BENKMAN, C.W., W.C. HOLIMON, AND J.W. SMITH. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. *Evolution* 55:282–294.
- BOGGS, C.L., W.B. WATT, AND P.R. EHRlich, EDS. 2003. *Butterflies: Ecology and Evolution Taking Flight*. University of Chicago Press, Chicago, Illinois.
- BOHANNAN, B.J.M., AND J.B. HUGHES. 2003. New approaches to analysing microbial biodiversity data. *Current Opinion in Microbiology* 6:282–287.
- BRUSSARD, P.F., J.F. BAUGHMAN, D.D. MURPHY, AND P.R. EHRlich. 1989. Complex population differentiation in checkerspot butterflies (*Euphydryas* spp.). *Canadian Journal of Zoology* 67:330–335.
- BRUSSARD, P.F., P.R. EHRlich, D.D. MURPHY, B.A. WILCOX, AND J. WRIGHT. 1985. Genetic distances and the taxonomy of checkerspot butterflies (Nymphalidae: Nymphalinae). *Journal of the Kansas Entomological Society* 58:403–412.

- BUSH, G.L. 1994. Sympatric speciation in animals: New wine in old bottles. *TREE* 9:285–288.
- CLARIDGE, M.F. 1995. Species and speciation. *TREE* 10:38.
- CLARIDGE, M.F., H.A. DAWAH, AND M.R. WILSON, EDS. 1997. *Species: The Units of Biodiversity*. Chapman and Hall, London, England.
- COYNE, J.A. 1992. Genetics and speciation. *Nature* 355:511–515.
- CRACRAFT, J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1:159–187.
- DAILY, G.C., ed. 1997. *Nature's Services*. Island Press, Washington, DC, USA.
- DAILY, G.C., AND P.R. EHRLICH. 1996a. Global change and human susceptibility to disease. *Annual Review of Energy and the Environment* 21:125–144.
- DAILY, G.C., AND P.R. EHRLICH. 1996b. Nocturnality and species survival. *Proceedings of the National Academy of Sciences USA* 93:11709–11712.
- DAILY, G.C., AND K. ELLISON. 2002. *The New Economy of Nature: The Quest to Make Conservation Profitable*. Island Press, Washington, D.C.
- DARWIN, C. 1859. *On the Origin of Species*. John Murray, London, England, UK.
- DAVIS, J.I. 1996. Phylogenetics, molecular variation, and species concepts. *BioScience* 46:502–511.
- DE QUEIROZ, K. 1998. The general lineage concept of species, species criteria, and the process of speciation. Pages 57–75 in D.J. Howard and S.H. Berlocher, eds., *Endless Forms: Species and Speciation*. Oxford University Press, Oxford, England, UK.
- DE QUEIROZ, K., AND M.J. DONOGHUE. 1988. Phylogenetic systematics and the species problem. *Cladistics* 4:317–338.
- DEVRIES, P.J. 1987. *The Butterflies of Costa Rica and Their Natural History: Papilionidae, Pieridae, Nymphalidae*. Princeton University Press, Princeton, New Jersey, USA.
- DEWEERDT, S. 2002. What really is an evolutionarily significant unit? The debate over integrating genetics and ecology in conservation biology. *Conservation Biology in Practice* 3:10–17.
- DOBZHANSKY, T. 1937. *Genetics and the Origin of Species*. Columbia University Press, New York, New York, USA.
- DONOGHUE, M.J. 2001. A wish list for Systematic Zoology. *Systematic Biology* 50:755–757.
- DUNN, C.P. 2003. Keeping taxonomy based in morphology. *TREE* 18:270–271.
- EHRLICH, P.R. 1961a. Has the biological species concept outlived its usefulness. *Systematic Zoology* 10:167–176.
- EHRLICH, P.R. 1961b. Systematics in 1970: Some unpopular predictions. *Systematic Zoology* 10:157–158.
- EHRLICH, P.R. 1964. Some axioms of taxonomy. *Systematic Zoology* 13:109–123.
- EHRLICH, P.R. 1997. *A World of Wounds: Ecologists and the Human Dilemma*. Ecology Institute, Oldendorf/Luhe, Germany.
- EHRLICH, P.R. 2000. *Human Natures: Genes, Cultures, and the Human Prospect*. Island Press, Washington, D.C.
- EHRLICH, P.R. 2001. Tropical butterflies: A key model group that can be “completed”. *Lepidoptera News* 2:1, 10–12.
- EHRLICH, P.R. 2002. Human natures, nature conservation, and environmental ethics. *BioScience* 52:31–43.
- EHRLICH, P.R., AND G.C. DAILY. 1993. Population extinction and saving biodiversity. *Ambio* 22:64–68.
- EHRLICH, P.R., AND A.H. EHRLICH. 1991. *Healing the Planet*. Addison-Wesley, Reading, Massachusetts, USA.
- EHRLICH, P.R., AND A.H. EHRLICH. 2004. *One with Nineveh: Politics, Consumption, and the Human Future*. Island Press, Washington, DC, USA.
- EHRLICH, P.R., AND I. HANSKI. 2004. *On the Wings of Checkerspots: A Model System for Population Biology*. Oxford University Press, Oxford, England, UK.
- EHRLICH, P.R., I. HANSKI, AND C.L. BOGGS. 2004. What have we learned? Pages 288–300 in P.R. Ehrlich and I. Hanski, eds., *On the Wings of Checkerspots: A Model System for Population Biology*. Oxford University Press, London, England, UK.
- EHRLICH, P.R., AND R.W. HOLM. 1962. Patterns and populations. *Science* 137:652–657.
- EHRLICH, P.R., AND D.D. MURPHY. 1981. Butterfly nomenclature: A critique. *Journal of Research on the Lepidoptera* 20:1–11.
- EHRLICH, P.R., AND P.H. RAVEN. 1969. Differentiation of populations. *Science* 65:1228–1232.

- EHRlich, P.R., AND R.R. WHITE. 1980. Colorado checkerspot butterflies: Isolation, neutrality, and the biospecies. *American Naturalist* 115:328–341.
- EHRlich, P.R., R.R. WHITE, M.C. SINGER, S.W. McKECHNIE, AND L.E. GILBERT. 1975. Checkerspot butterflies: A historical perspective. *Science* 188:221–228.
- FEILD, T.S., N.C. ARENS, AND T.E. DAWSON. 2003. The ancestral ecology of angiosperms: emerging perspectives from extant basal lineages. *International Journal of Plant Sciences* 164:S129–S142.
- FELSENSTEIN, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- FLEISHMAN, E., R. MACNALLY, AND J.P. FAY. 2003. Validation tests of predictive models of butterfly occurrence based on environmental variables. *Conservation Biology* 17:806–817.
- FRIEDMAN, W.E., AND S.K. FLOYD. 2001. Perspective: The origin of flowering plants and their reproductive biology — a tale of two phylogenies. *Evolution* 55: 217–231.
- GHISELIN, M.T. 1975. A radical solution to the species problem. *Systematic Zoology* 23:536–544.
- GILLHAM, N.W. 1965. Geographic variation and the subspecies concept in butterflies. *Systematic Zoology* 5:100–120.
- GORDON, D. 1999. *Ants at Work: How an Insect Society is Organized*. The Free Press, New York, New York.
- GRANT, B.R., AND P.R. GRANT. 1997. Genetics and the origin of bird species. *Proceedings of the National Academy of Sciences USA* 94:7768–7775.
- HARRISON, R.G. 1998. Linking evolutionary pattern and process: The relevance of species concepts for the study of speciation. Pages 19–31 in D.J. Howard and S.H. Berlocher, eds., *Endless Forms: Species and Speciation*. Oxford University Press, New York, New York, USA.
- HARVEY, P.H., A.J. LEIGH BROWN, J.M. SMITH, AND S. NEE, EDS. 1996. *New Uses for New Phylogenies*. Oxford University Press, Oxford, England, UK.
- HASSANIN, A., AND E. DOUZERY. 2003. Molecular and morphological phylogenies of Ruminantia and the alternative position of the Moschidae. *Systematic Biology* 52:206–228.
- HENDRICKSON, J.A., AND P.R. EHRlich. 1971. An expanded concept of “species diversity.” *Notulae Naturae* 439:1–6.
- HEY, J. 2001. *Gene, Categories, and Species*. Oxford University Press, New York, New York, USA.
- HOCHBERG, M.E., AND M. VAN BAALEN. 1998. Antagonistic coevolution over productivity gradients. *American Naturalist* 152:620–634.
- HÖLDOBLER, B., AND E.O. WILSON. 1990. *The Ants*. Harvard University Press, Cambridge, Massachusetts.
- HORNER-DEVINE, M.C., K.M. CARNEY, AND B.J.M. BOHANNAN. 2004. An ecological perspective on bacterial diversity. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 271:113–122.
- HORNER-DEVINE, M.C., M.A. LEIBOLD, V.H. SMITH, AND B.J.M. BOHANNAN. 2003. Bacterial diversity patterns along a gradient of primary productivity. *Ecology Letters* 6:613–622.
- HUGHES, J.B., G.C. DAILY, AND P.R. EHRlich. 1997. Population diversity: Its extent and extinction. *Science* 278:689–692.
- HUGHES, J.B., G.C. DAILY, AND P.R. EHRlich. 1998. The loss of population diversity and why it matters. Pages 71–83 in P.H. Raven, ed., *Nature and Human Society*. National Academy Press, Washington, DC, USA.
- HUGHES, J.B., G.C. DAILY, AND P.R. EHRlich. 2000. Conservation of insect diversity: A habitat approach. *Conservation Biology* 14:1788–1797.
- HULL, D.L. 1976. Are species really individuals? *Systematic Zoology* 25:174–191.
- HULL, D.L. 1997. The ideal species concept — and why we can’t get it. Pages 357–380 in M.F. Claridge, H.A. Dawah, and M.R. Wilson, eds., *Species: The Units of Biodiversity*. Chapman and Hall, London, England.
- HUXLEY, J., ED. 1940. *The New Systematics*. Oxford University Press, London, England, UK.
- KAUFMAN, L.S., C.A. CHAPMAN, AND L.J. CHAPMAN. 1997. Evolution in fast forward: Haplochromine fishes of the Lake Victoria region. *Endeavour* (London) 21:23–30.
- KING, M.-C., AND A.C. WILSON. 1975. Evolution at two levels in humans and chimpanzees. *Science* 188:107–116.
- KRINGS, M., A. STONE, R.W. SCHMITZ, H. KRAINITZKI, M. STONEKING, AND S. PAABO. 1997. Neandertal DNA sequences and the origin of modern humans. *Cell* 90:19–30.
- LINNAEUS, C. 1758. *Systema Naturae. Regnum Animale*, 10th Edition. Engelmann, Leipzig, Germany.
- LIPSCOMB, D., N. PLATNICK, AND Q. WHEELER. 2003. The intellectual content of taxonomy: A comment on

DNA taxonomy. *TREE* 18:65–66.

- LUCK, G., G.C. DAILY, AND P.R. EHRLICH. (In press.) The multiple dimensions of population diversity. *Trends in Ecology and Evolution*.
- MALLET, J. 1995. A species definition for the modern synthesis. *Trends in Ecology and Evolution* 10:294–299.
- MALLET, J., AND K. WILLMOTT. 2003. Taxonomy: Renaissance or Tower of Babel? *Trends in Ecology and Evolution* 18:57–59.
- MAY, R.M. 1988. How many species are there on Earth? *Science* 241:1441–1449.
- MAYDEN, R.L. 1997. A hierarchy of species concepts: The denouement in the saga of the species problem. Pages 381–424 in M.F. Claridge, H.A. Dawah, and M.R. Wilson, eds., *Species: The Units of Biodiversity*. Chapman and Hall, London, England, UK.
- MAYR, E. 1942. *Systematics and the Origin of Species*. Columbia University Press, New York, New York.
- MAYR, E., ED. 1957. *The Species Problem*. American Association for the Advancement of Science, Washington, DC, USA.
- MAYR, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge, Massachusetts.
- MAYR, E., AND J.M. DIAMOND. 2001. *The Birds of Northern Melanesia: Speciation, Ecology, and Biogeography*. Oxford University Press, Oxford, England, UK.
- MAYR, E., E.G. LINSLEY, AND R.L. USINGER. 1953. *Methods and Principles of Systematic Zoology*. McGraw-Hill Book Company, New York, New York, USA.
- MEEGASKUMBURA, M., F. BOSSUYT, R. PETHIYAGODA, K. MANAMENDRA-ARACHCHI, M. BAHIR, M.C. MILINKOVITCH, AND C.J. SCHNEIDER. 2002. Sri Lanka: An amphibian hot spot. *Science* 298:379.
- MICHENER, C.D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Harvard University Press, Cambridge, Massachusetts, USA.
- MICHENER, C.D. 2000. *The Bees of the World*. Johns Hopkins University Press, Baltimore, Maryland.
- MISCHLER, B.D., AND M.J. DONOGHUE. 1982. Species concepts: A case for pluralism. *Systematic Zoology* 31:491–503.
- MISHLER, B., S. ASKAY, C. WEBB, D. ACKERLY, R. MOE, AND S. MARKOS. 2003. Phylogenetically structured databases: The future of bioinformatics. *Botanical Society of America Abstract*.
- MORITZ, C. 1994. Defining “evolutionarily significant units” for conservation. *Trends in Ecology and Evolution* 9:373–375.
- MURPHY, D.D., AND P.R. EHRLICH. 1983. Crows, bobs, tits, elves and pixies: The phoney “common name” phenomenon. *The Journal of Research on the Lepidoptera* 22:154–158.
- NAVARRO, A., AND N.H. BARTON. 2003. Chromosomal speciation and molecular divergence — accelerated evolution in rearranged chromosomes. *Science* 300:321–324.
- NIXON, K.C., AND Q.D. WHEELER. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.
- OLIVER, I., AND A.J. BEATTIE. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology* 7:562–568.
- OLIVER, I., AND A.J. BEATTIE. 1996a. Designing a cost-effective invertebrate survey: A test of methods for rapid assessment of biodiversity. *Ecological Applications* 6: 594–607.
- OLIVER, I., AND A.J. BEATTIE. 1996b. Invertebrate morphospecies as surrogates for species: A case study. *Conservation Biology* 10:99–109.
- ORR, A. 2001. The genetics of specied differences. *TREE* 16:343–350.
- ORR, M.R., AND T.B. SMITH. 1998. Ecology and Speciation. *TREE* 13:502–506.
- PACE, N.R. 1997. A molecular view of microbial diversity and the biosphere. *Science* 276:734–740.
- PALUMBI, S.R., AND F. CIPRIANO. 1998. Species identification using genetic tools: The value of nuclear and mitochondrial gene sequences in whale conservation. *Journal of Heredity* 89:459–464.
- PATTERSON, H.E.H. 1985. The recognition concept of species. Pages 21–29 in E.S. Vrba, ed., *Species and Speciation*. Transvaal Museum, Pretoria, South Africa.
- PEARSON, D.L., AND F. CASSOLA. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): Indicator taxon for biodiversity and conservation studies. *Conservation Biology* 6:376–391.
- PENNISI, E. 2001. Linnaeus’s last stand? *Science* 291:2304–2307.
- PENNISI, E. 2003. Charting the evolutionary history of life. *Science* 300:1691–1697.

- PENZ, C.M. 1999. Higher level phylogeny for the passion-vine butterflies (Nymphalidae, Heliconiinae) based on early stage and adult morphology. *Zoological Journal of the Linnean Society* 127:277–344.
- PENZ, C.M., AND P.J. DeVRIES. 2003. Phylogenetic analysis of Morpho butterflies (Nymphalidae, Morphinae): Implications for classification and natural history. *American Museum Novitates* 3374:1–33.
- RAVEN, P.H. 1978. Future directions in plant population biology. Pages 461–482 in O.T. Solbrig, S.K. Jain, G.B. Johnson, and P.H. Raven, eds., *Topics in Plant Population Biology*. Columbia University Press, New York, New York, USA.
- RAVEN, P.H. 1980a. Hybridization and the nature of species in higher plants. *Canadian Botanical Association Bulletin* 13 (Supplement):3–10.
- RAVEN, P.H., ED. 1980b. *Research Priorities in Tropical Biology*. National Research Council, Committee on Research Priorities in Tropical Biology, National Academy of Sciences, Washington, DC, USA.
- RAVEN, P.H., AND E.O. WILSON. 1992. A fifty-year plan for biodiversity surveys. *Science* 258:1099–1100.
- REISEBERG, L.H. 2001. A genic view of species integration. *Journal of Evolutionary Biology* 14:883–886.
- REISEBERG, L.H., AND J.M. BURKE. 2001. The biological reality of species: Gene flow, selection, and collective evolution. *Taxon* 50:235–255.
- REISEBERG, L.H., AND K. LIVINGSTONE. 2003. Chromosomal speciation in primates. *Science* 300:267–268.
- RUSE, M. 1987. Biological species: Natural kinds, individuals, or what? *British Journal for the Philosophy of Science* 38:225–242.
- RYDER, O.A. 1986. Species conservation and systematics: The dilemma of subspecies. *TREE* 1:9–10.
- SCHWARZBACH, A.E., AND L.H. REISEBERG. 2002. Likely multiple origins of a diploid sunflower species. *Molecular Ecology* 11:1703–1715.
- SCOTT, J.A. 1986. *The Butterflies of North America: A Natural History and Field Guide*. Stanford University Press, Stanford, California, USA.
- SEBERG, O., C.J. HUMPHRIES, S. KNAPP, D.W. STEVENSON, G. PETERSEN, N. SCHARFF, AND N.M. ANDERSEN. 2003. Shortcuts in systematics? A commentary on DNA-based taxonomy. *TREE* 18:63–65.
- SEKERCIOGLU, C.H. 2002. Impacts of birdwatching on human and avian communities. *Environmental Conservation* 29:282–289.
- SISK, T.D., A.E. LAUNER, K.R. SWITKY, AND P.R. EHRlich. 1994. Identifying extinction threats. *BioScience* 44:592–604.
- SOKAL, R.R., AND T.J. CROVELLO. 1970. The biological species concept: A critical evaluation. *The American Naturalist* 104:127–153.
- SPEERLING, F.A.H. 2003. Butterfly molecular systematics: From species definitions to higher-level phylogenies. Pages 431–458 in C.L. Boggs, W.B. Watt, and P.R. Ehrlich, eds., *Butterflies: Ecology and Evolution Taking Flight*. University of Chicago Press, Chicago, Illinois, USA.
- STERELNY, K., AND P.E. GRIFFITHS. 1999. *Sex and Death: An Introduction to the Philosophy of Biology*. University of Chicago Press, Chicago, Illinois, USA.
- STROH, M. 2003. Uncovering hidden species. *Baltimore Sun*, May 26, 2003.
- TAUTZ, D., P. ARCTANDER, A. MINELLI, R.H. THOMAS, AND A.P. VOGLER. 2003. A plea for DNA taxonomy. *TREE* 18:70–74.
- THOMAS, J.A., M.G. TELFER, D.B. ROY, C.D. PRESTON, J.J.D. GREENWOOD, J. ASHER, R. FOX, R.T. CLARKE, AND J.H. LAWTON. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303:1879–1881.
- THOMPSON, J.N. 1994. *The Coevolutionary Process*. University of Chicago Press, Chicago, Illinois, USA.
- THOMPSON, J.N., AND B.M. CUNNINGHAM. 2002. Geographic structure and dynamics of coevolutionary selection. *Nature* 417:735–738.
- TURELLI, M., N. BARTON, AND J.A. COYNE. 2001. Theory and speciation. *TREE* 16:330–343.
- VANE-WRIGHT, R.I., C.J. HUMPHRIES, AND P.H. WILLIAMS. 1991. What to protect? Systematics and the agony of choice. *Biological Conservation* 55:235–254.
- VIA, S. 2001. Sympatric speciation in animals: The ugly duckling grows up. *TREE* 16:381–390.
- VOGLER, A.P., AND R. DESALLE. 1994. Diagnosing units of conservation management. *Conservation Biology* 8:354–363.
- VRANA, P., AND W. WHEELER. 1992. Individual organisms as terminal entities: Laying the species problem to

- rest. *Cladistics* 8:67–72.
- WAHLBERG, N., AND M. ZIMMERMANN. 2000. Pattern of phylogenetic relationships among members of the tribe Melitaeini (Lepidoptera: Nymphalidae) inferred from mtDNA sequences. *Cladistics* 16:347–363.
- WATT, W.B., C.W. WHEAT, E.H. MEYER, AND J.-F. MARTIN. 2003. Adaptation at specific loci. VII. Natural selection, dispersal, and the diversity of molecular-functional variation patterns among butterfly species complexes (Colias: Lepidoptera, Pieridae). *Molecular Ecology* 12:1265–75.
- WILSON, E.O., AND W.L. BROWN. 1953. The subspecies concept and its taxonomic application. *Systematic Zoology* 2:97–111.
- WINKER, K. 2004. Natural history museums in a postbiodiversity era. *BioScience* 54:455–459.
- WU, C.-I. 2001. The genic view of the process of speciation. *Journal of Evolutionary Biology* 14:851–865.
- YATES, T.L., J.N. MILLS, C.A. PARMENTER, T.G. KSIAZEK, R.R. PARMENTER, J.R. VANDE CASTLE, C.H. CALISHER, S.T. NICHOL, K.D. ABBOTT, J.C. YOUNG, M.L. MORRISON, B.J. BEATY, J.L. DUNNUM, R.J. BAKER, J. SALAZAR-BRAVO, AND C.J. PETERS. 2002. The ecology and evolutionary history of an emergent disease: hantavirus pulmonary syndrome. *BioScience* 52:989–998.
- ZANGERL, A.R., AND M.R. BERENBAUM. 2003. Phenotype matching in wild parsnip and parsnip webworms: Causes and consequences. *Evolution* 57:806–815.